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THE CLASSIFICATION OF INSECTS ON THE CHARACTERS OF THE LARVA AND PUPA.[1]

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Knowledge of the preparatory stages of insects is still very fragmentary in comparison with the much more extensive information available concerning the comparative structure and classification of the imaginal forms. These developmental stages are of great interest, however, and have been neglected only for practical reasons incident to the vast extent of insects as a group, and the impossibility of correlating the adult and preparatory stages without the laborious process of breeding each individual species.

A comparative study of insect larvæ and pupæ throws much light on the origin and development of metamorphosis, a condition which reaches its climax in the highly specialized insect. It is also essential to an understanding of the varied adaptations of insects, many of which appear in such a form that their biological significance cannot otherwise be recognized. The independent adaptations of insect larvæ are peculiar phenomena, which must aid greatly in the application of the biogenetic law to insects; in fact any attempt to correlate insect ontogeny with phylogeny must be undertaken with careful attention to the characteristics of larval development. Such functional and structural modifications in larval insects, have I think, not received the attention which they deserve. They have usually been considered as phenomena without close counterpart among other animals, or at least as such an exaggerated expression of metamorphic development that they could not readily be re-

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duced to simpler terms. Many entomologists have of course traced the very evident progress of metamorphosis, from the rather gradual series of changes shown in the ontogeny of the more primitive insects, to the highly adaptive, saltatory process exhibited by members of several of the greatly specialized orders, and have interpreted metamorphosis on a physiological basis.

Before entering into a discussion of those characteristics of insect larvæ and pupæ which are of interest from a taxonomic standpoint, I hope I may be pardoned for calling attention to several oft-repeated groups of facts relating to insects in general. Insects stand apart from other animals in several particulars. They include a great wealth of species, known mainly in the adult stage through the labors of a large number of systematic entomologists. In spite of the fact that these workers have described an almost unbelievably large number of living species, the insect fauna of every zoölogical region is still so imperfectly known that, not only are many new species and genera discovered each year, but entirely new families and even new orders, are most unexpectedly brought to light. Thus, at least two new orders of insects have been found within the past ten years, while in the same period three very clearly defined families have been added to the well-known order Hymenoptera. The great variety of insects is undoubtedly due to their having appropriated practically every sort of environment. Thus, aside from the large number of terrestrial forms adapted for aërial life in their perfect condition, many are amphibiotic, or even purely aquatic during either a part or during the whole of their life-cycle. Others have become epiphytic or epizoic, with the great modifications attendant upon this mode of life. Some are internal parasites, most generally of other insects, either in their preparatory stages, or more rarely, during their entire life. Highly predatory species, comparable to the birds and beasts of prey, are also numerous, and examples of many other striking methods of life will readily occur to one after a moment's thought. The comparative anatomy of insects may be studied much more readily than that of most other groups of animals, since the skeletal elements are external in position, where they may readily be studied in the most minute details. This condition finds no

other close parallel in other groups of animals. It is true that the shells of molluscs, the tests of echinoderms, or the external armor of reptiles present features in common, but they do not exhibit in combination, the high degree of adaptiveness and the great variety of modification seen in the exoskeleton of insects. Crustacea make the closest approach to this condition, but these animals are greatly restricted in many ways by their more uniform aquatic environment.

It is, of course, in relation to their metamorphosis, with the interpolation of such dissimilar preparatory stages, that insects find one of their greatest opportunities for functional and structural modification. In consequence, we find that the larvæ exhibit a greater degree of plasticity than do the imagines. Apart from the comparatively short period during which the adults exercise their reproductive functions, the important activities of the higher insects are restricted to the usually much prolonged period of larval development. This period s largely concerned with the growth through which adult size is reached, and growth practically stops in almost all insects at the completion of the final larval instar. Although the beginnings of the purely imaginal organs may appear often quite early in larval development, they do not assume much physiological importance until the pupal stage, at which time the relations of the insect and its external surroundings suddenly decrease almost to the vanishing point, and all activities are closely bound up in the profound internal changes necessary to bridge the gap between larva and imago.

It is, therefore, clear that the trophic functions dominate the larva as most essential to its growth, and it appears that the characteristics of the larval stages may usually be interpreted with this in view. That the larva shows the greatest plasticity will I think be evident from an examination of the structure of the larvæ of the several groups. The pupa on the other hand is the most uniform stage, a condition which may be readily attr - buted to its much reduced relations with its environment and the slight peculiarities of some pupæ are usually directly correlated with the few activities which they do exhibit toward external conditions.

The modifications of the imaginal insect naturally show much greater complexity, and are far less easily to be correlated with any group of activities. It can be accepted as a general principle also, that they are in great part seemingly less directly due to the environment, excluding, of course, certain features like those related to oviposition, hypogæic life, etc. In spite of many apparently exuberant structural characters, frequent greatly exaggerated development of certain parts, and occasional extreme secondary simplification, the imaginal condition is far more stable. This is most readily appreciated by taxonomists, who experience far less difficulty in delimiting large groups on the basis of adults than they do in attempting a similar treatment of larvæ.

The wide applicability of recapitulation and the biogenetic law to the ontogeny animals in general is so clear that its importance as a fundamental principle cannot be discounted. The exact nature of the parallelism between phylogeny and ontogeny has always been the basis for divergent views on the part of biologists, who have readily accepted its existence, and its origin as a part of the evolutionary process. It has been applied with much general success to the embryogeny of the vertebrates and of many invertebrates. In many cases of invertebrates that exhibit striking metamorphosis, like crustaceans and echinoderms, at least some features of the post-embryonic development fall readily in line with the more continuous process of recapitulation in the vertebrate embryo.

It is with the metabola among insects that we find the intiation of an almost entirely discontinuous process in development, interpolated between the embryonic development and the sexually mature condition. This is most strikingly illustrated by an insect such as the common housefly. During the embryogeny, the rudiments of antennæ, legs and other appendages appear, and give every indication that they will pass over continuously into the homologous parts of the imago. During these stages the embryo undoubtedly reproduces what we consider to have been the original condition in the ancestors of insects, particularly in reference to the metameric disposition of the parts and appendages of the head. In a more generalized nsect we find the

imaginal form evolved directly from these initial stages. In the fly, however, as in other specialized insects we find the newly hatched larva almost destitute of morphological indications of most of the appendages which reappear much later in larval life as histoblasts that represent the rudiments of the imaginal appendages.

However, we may regard the interpretation of the biogenetic law as applied to other animals, it is evident that many insects exhibit a very distorted development when viewed from this standpoint. This matter has been treated already by Janet in his "Ontogenèse de l'insecte" ('09). The taxonomist, who is continually brought into contact with the permutations of various single characters, soon begins to regard species as made up of, or at least most easily definable, by series of single clear-cut characters. His attitude is also closely parallel to that of the geneticist who finds that he must attack his problems through the behavior of unit characters. Cope ('95) early called attention to the dependence of the taxonomist upon single characters in his discussion of the biogenetic law as applied to vertebrates.

In a series of papers, which have been gathered together in his "Biologie Générale" ('11), Giard ('92–'05) described certain peculiar phenomena of development which he termed pœcilogony. Among several widely separated groups of animals, certain isolated species show modifications in their ontogeny whereby two widely different types of development give rise to individuals belonging presumably to the same species. This appears frequently to be independent of any alternation of generations and occurs in forms of many well-known genera. Giard regards some cases of pœcilogony from the standpoint of their probable origin as seasonal pœcilogony, geographic pœcilogony or as ethological pœcilogony. How far these phenomena can be regarded as the expression of a single principle is somewhat doubtful, since the significance of the alternation of generations that occurs to such a widely different extent in several groups of insects is by no means clear. Also, de Meijere ('10) and others have shown that the polymorphism of certain Lepidoptera follows Mendel's law in inheritance and that the characteristics of the different forms of female in *Papilio* behave as unit characters.

Such cannot be true of geographic pœcilogony, but however the origin and preservation of the several types of pœcilogenetic development may be explained, the outstanding fact remains that intraspecific pœcilogony occurs. This is of interest in the present connection as it shows that enormous changes in development may readily appear in the early stages of an animal without impressing themselves upon the later stages.

When applied to groups of insects rather than to single species, Giard's views assume great interest from the standpoint of the larval and pupal stages. If two groups of individuals of a single species can reach the adult stage by separate paths, it is seen that we have a much simpler case of apparently similar nature where groups of species have developed highly adaptive methods of development which are far from what might be expected if their development had proceeded along the more conventional lines of ancestral recapitulation.

I shall not digress to attempt any discussion of the origin of metamorphosis in insects nor of the way in which its increasing complexity can be traced in living insects, from those showing its primitive absence to others like the fly referred to above, in which the larva is wholly unlike the imago not only in structure, but in physiology and in its different ethological relationship to a dissimilar environment. From the present standpoint, the hypermetamorphosis of many insects is of especial interest and I shall refer to this subject later.

The properly trained zoölogist is greatly outraged if he should see a paper dealing with the larvæ of certain insects "classified as independent organisms," and will probably go no further to inquire into the viewpoint of the writer. This is very natural when we regard the whole animal and plant world as so closely interdependent that a change in the abundance or distribution of one species soon shows its effect upon a great number of others, whose relations to the first species may not have been thought of previously. Viewed in the light of pœcilogeny, or even after one has worked for some time upon the classification of the highly modified larvæ of some group of insects, it becomes far from an absurdity and the more closely we inquire into the matter the more clearly does it appear that many problems re-

lating to insect larvæ may be profitably dealt with without taking into account the adult insects. This is particularly true with taxonomic studies, for these, when used with due caution, are very valuable in modifying any conclusions based upon studies of the adults.

Even the eggs of insects furnish characters which are suitable for taxonomic treatment. Like the later stages, the eggs commonly show distinctive features in the form and structure of the chitinous shell, aside from the contained embryo. Like the similarly large eggs of birds, they are frequently characteristically colored, although a spotting or color pattern is rather rare among insect eggs. The relation of color development to environment is nicely illustrated by the eggs, as only such as are deposited in places exposed to the light show a color other than that imparted by the whitish or buff-colored yolk. The color often changes where the shell is transparent, as the developing color of the larva is to be seen through the shell. Whether the color of insect eggs may be interpreted on the basis of protective or warning color seems very doubtful. In certain bright yellow or orange eggs, as for example those of many chrysomelid beetles the color may be due to shell color or only to the brightly colored yolk. There seems not to be sufficient uniformity in egg-color, however, to attempt any explanation of its probable function.

The eggs of Lepidoptera, especially those of the butterflies, have received more attention than those of any other insects. Externally these are commonly of unusually complex sculpture, with surface reticulation or areolation, sometimes assuming the form of longitudinal and transverse ribs. Scudder ('89) has shown the possibility of classifying the eggs of some of our North American butterflies, and Tutt ('05–'06) gives an interesting résumé of the egg-structure of some of the groups of British butterflies. According to Tutt, the eggs of the various species of any given family are almost always similar, although varying in detail in the several forms. Thus, the Thymelicid eggs are flat with three axes of different lengths, differing from those of the other groups which are circular in horizontal section. In the Urbicolid skippers they are somewhat more than hemispherical; in the Lycænids shallow, flattened, tiarate or echinoid;

in the Papilionids and some Satyrids almost globular; in the Pierids, long, slender and spindle-shaped; in the Nymphalids, somewhat barrel-shaped with projecting ribs reaching from base to apex, etc. In some butterfly eggs there is a well marked lid, defined by a weakened line in the shell, along which the shell ruptures on hatching, causing the lid to separate from the remainder of the shell. In the Hemipterous family Pentatomidæ a similar lid occurs, along the margin of which is a circle of spines or thorns. When the eggs of insects are better known, they will undoubtedly prove of great interest from a taxonomic standpoint. Incidentally, it is of more than passing interest to note that these organisms in such an early stage of ontogeny show visible external characters by which not only larger groups may be delimited, but which serve to distinguish the numerous species of some groups. In this connection, it must not be forgotten, however, that the egg-shell is really formed by the mother and is hence a direct product of the adult insect and not of the embryo, so that its high specialization cannot be attributed to any differentiation of the embryo. In this sense we are dealing with a matter of entirely different significance from that now to be presented in relation to insect larvæ.

Insect larvæ may be separated into several rather clearly defined types, and in at least one of the extensive orders, the larvæ of the great majority of the species included may be referred to a single, quite consistent type. Without question the most primitive of these is the campodeiform larvæ so named in recognition of its similarity to the imago of *Campodea*, a genus of Apterygote insects. Campodeiform larvæ appear with many modifications in several widely separated orders of insects. A second, quite consistent type, is caterpillar-like or eruciform, and larvæ of this kind prevail almost universally in the Panorpatæ and several orders which appear to have been derived from a Panorpate ancestral type. Various other types are also easily to be recognized, most of them of quite restricted occurrence and characteristic habitus. A vast residuum are either highly specialized in structure or greatly simplified through the loss of appendages and the acquisition of a vermiform body. These latter, so-called apodous larvæ, although quite uniform in gross

external appearance represent numerous independent lines of development.

In almost any group of insects there is easily seen the great ease with which adaptations in form appear, most commonly in response to the requirements of alimentation and respiration. Among these might be mentioned many grotesque modifications of the trophi of entomophagous parasites, the posterior closure of the alimentary tract, the great flattening of the body in many subcorticolous species, and the development of respiratory tubes, gills, etc., in aquatic forms. In details, the active, free-living types of larvæ naturally furnish the most striking and clear-cut characters, while those of sessile, or at least inactive habits show such a reduction or complexity in structrue, that they tend to converge toward a common type. There are notable exceptions to this last statement, however, as for example among the maggots of the higher Diptera to which I shall return later.

During recent years the larvæ of mosquitoes and those of some other Nematocerous Diptera, have been examined with perhaps greater care and thoroughness than those of any other insects. Were it not for this, no one should think of considering the highly specialized larvæ of this group before dealing with those of the more generalized insects. Mosquitoes are well-known as remarkably adaptive insects in many respects. The adult mosquito (at least the female) is phlebotomic and depends upon the higher vertebrates for its food. It further shows a complex relationship to its vertebrate food-reservoirs through the medium of certain Protozoan parasites. The malarial parasites of man undergo their definitive life cycle in the mosquito and the same is true of various other similar Protozoa parasitic in the hosts of other mosquitoes. As is well known to every one, the larvæ of mosquitoes are very active aquatic creatures of very peculiar, although quite uniform conformation. It is perhaps not so well known that many of the species are restricted quite closely to certain places, *e. g.*, ponds, pools, rain-barrels, brackish water, permanent water, temporary water, etc., in such a way as to show that they thrive ordinarily only under quite specific conditions. Nearly all are surface breathers and are equipped with a breathing tube into which the main lateral tracheal trunks

extend, and which they thrust through the surface of the water for respiration. The mosquito larvæ is by no means unique among the lower Diptera in the general plan of its body although it is the most highly specialized in several respects.

A close morphological study of the larvæ of a large number of mosquitoes has brought to light many interesting facts. Of approximately 400 species known from North and Central America, the larvæ of a very large majority are known and have been carefully examined. Comparative descriptions of a considerable number of these were published in 1906 by Dyar and Knab, and in their monograph on mosquitoes ('12–'17) Howard, Dyar and Knab have included a complete account of all of the known larvæ from this region. In the earlier paper ('06) the statement is made that "we are compelled to the conclusion that specific limits are more sharply defined, or at least more readily appreciable, in the larvæ of Culicidæ, than in the adults, although generic limitations are less sharply drawn." There seems to be no reason to change fundamentally this statement although it appears from the later and more extensive publication that its authors have been unable to find satisfactory diagnostic characters on the basis of larval structure for a small percentage of the recognized species. Such characters as they do employ in their keys are readily perceived and the identification of larval mosquitoes is far easier than that of the adults, at least for those not thoroughly familiar with the group.

The two (or sometimes, three) subfamilies of the Culicidæ as at present constituted, are readily separable on the basis of larval structure and the same is true of the two tribes of Culicinæ (true mosquitoes). So far as one may divest one's mind of preconceived notions, it would appear that the genera of the subfamilies would have been segregated in much the same manner if the adults had remained unknown. It appears quite certain, however, that the division of the tribes would have been different to some extent, as the Anopheline mosquitoes present a striking difference from the other members of the tribe in which they are placed, on account of their extremely short breathing tube. It must also be admitted that in the adult condition they are a very clearly characterized group.

From the keys included in the monograph, it appears that in a number of cases, the larvæ do not fall readily into the linear arrangement of species adopted.

From the foregoing much abbreviated and necessarily incomplete account, it is very evident that the larvæ of mosquitoes exhibit morphological differences approximating in extent and fixity those characterizing the adults of the several species, and that a scheme of classification based on larval structures runs quite parallel with one based upon the imagines. In the case of these insects the larvæ show little differentiation in color and other superficial details, and the recognition characters are essentially those of structure.

In the pupæ of mosquitoes the development of specific, generic or tribal character is very limited and the identification of species in this stage is not satisfactory. This is quite like the condition in other groups of insects, although mosquitoes and related forms are almost the only insects with an active pupa. The activity of the pupa even in this case, is of course only a limited retention of the great activity of the larva, necessitated by its adjustment to aquatic life. The mosquito pupa breathes in a manner similar to the larva, by a pair of spiracular tubes that are thrust above the surface of the water, and although these organs emanate from the anterior part of the thorax in the pupa, this stage must remain highly active in order to perform its respiratory function.

Much attention has also been given to the systematic description and classification of the larvæ and pupæ of the other more generalized families of Diptera related to the mosquitoes by Osten Sacken ('62), Brauer ('83), Hart ('95), Johannsen ('03–'05) and numerous other entomologists. Quite recently Malloch ('17) has gathered together this information relating to American species and supplemented it with much new material. In these other families, the larvæ of the numerous species may very generally be easily distinguished and tabulated upon much the same type of characters as have been used for the mosquitoes. The genera and families are also separable on the same basis although the tabulation of the families is more difficult, indicating that the natural affinities are well indicated in the preparatory stages. In fact the correlation between the two is

very close, even to the difficulty of distinguishing two closely related groups. This is illustrated by the families Chrironomidæ and Ceratopogonidæ, separated in the imagines only by the blood-sucking habits and consequently modified mouthparts of the last family, and not readily characterized in the larval stage by mutually exclusive characters. The same condition is true of two divisions (Tipulidæ and Limnobiidæ) of the old family Tipulidæ. In all of these families more difficulty is met with in classifying the pupæ, as we have seen to be the case in the more completely known family of mosquitoes.

All of the Diptera so far referred to are not so highly specialized as many other families of the order, although among insects in general the Diptera must be regarded as structurally the most specialized group. Those which we have described, known as the Nematocera, retain in the larval condition some features of the generalized insect, notably in the well developed, free head, with the mandibles moving in opposition in a horizontal plane. To disregard for the moment the families of somewhat intermediate structure, and to turn to the higher Diptera, or Cyclorrhapha, we find larvæ of a very different type. They are maggot-like, microcephalic, with the head not differentiated and without appendages, with a simple internal framework, the cephalophyrangeal skeleton, that bears vertical, hook-like, non-opposable mandibles. Through almost the entire series of families, and in innumerable species, the larvæ present almost exactly the same appearance, with only the occasional development of some striking features (*e. g.*, in the genus *Fannia*, which has some elaborate tegumentary appendages). In these larvæ, only the posterior pair of spiracles are functional. These, however, are large, and each is provided with three slits. The form, size, and position of the spiracles, and the form, size, position, length, curvature and microscopic structure of the slits present such a complex series of permutations, that these organs in connection with certain cuticular structures, usually associated with the spiracular plates, serve for the identification of very many species. The value of these structures has long been recognized as valuable in classification and they have been carefully figured and described for a large number of species. Certain authors, notably

Portschinski (several papers), Osten Sacken ('87), Blanchard ('93–'96), Banks ('12), MacGregor ('14), and Rodhain and Bequaert ('16) have dealt with some of these larvæ in a way which is of interest in the present connection. As the specific characters in these flies relate to so few structures, it is very difficult to delimit the larger groups such as families, although the species appear in great measure to have individual characteristics of easy recognition.

The classification of the several families of flies related to the Muscidæ has been the cause of much controversy among entomologists and there is no question concerning the advisability of utilizing the larvæ in any attempt to elucidate their natural affinities. Not excepting any animals, the species of some of these families are distinguished by the most minute characters, so slightly do the adults vary in structure. In very many cases, it is already known that the larvæ show more striking differences, but it would be unwise at the present time to do more than to predict that a comparison of adult and larval structure and of habits and behavior in these insects, which appear to be undergoing a rapid evolution, will lead to results of great interest.

Another group of insects in which it is possible to trace the probable course of larval modification in the form of several series is seen in the Trichoptera, Lepidoptera and Hymenoptera. These orders appear to have been developed rather directly from a group similar to the Panorpatæ or Mecoptera which is represented, although not very extensively in the living fauna. In these several orders the larva is primarily of the eruciform type, but becomes apodous in some cases, more generally so in the Hymenoptera, where only a small series of families retain the caterpillar-like larva.

Of all larval insects, the caterpillars of various butterflies and moths are best known to the casual observer and they have long attracted the attention of naturalists. In general form they are remarkably uniform, with long cylindrical body, well developed head capsule and trophi, functional thoracic legs and a series of prolegs on certain segments of the abdomen differing greatly in structure from the thoracic ones, but homologous with them. In only a few Lepidoptera do the larvæ become apodous or nearly

so. The majority of caterpillars occur upon their food plants in exposed situations, and as they are very helpless creatures, have developed in many cases elaborate spines, tufts of bristles, or poisonous hairs which are undoubtedly protective adaptations. Many of them are also remarkably colored, presenting shades and patterns that may be readily interpreted on the basis of the theories of protective resemblance, warning color and mimicry· Consequently, at first blush these larvæ would not appear to show any consistent characters applicable to their classification on a rational basis. In 1886 W. Müller found that the position of certain primary body-setæ might be utilized for the purpose of classification. Dyar ('94), Forbes ('10), Tsou ('14), and most recently Fracker ('15), have elaborated and modified this idea and it is now applicable in a most satisfactory way throughout almost the entire order. Thus we find that the arrangement of these setæ follows a certain plan, that the individual setæ are homologous, and that the modifications present in specialized families may be derived from those of more primitive groups. Still more interesting is the fact that very young larvæ of all groups tend to approach more closely to the primitive arrangement than the larvæ of later instars. We find thus quite evidently that in ontogeny the caterpillar reproduces certain changes in setal arrangement that have occurred in the phylogeny of the group. Fracker has called attention to this as he found it to occur quite consistently, although he fails to point out some of the interesting conclusions to which it may lead. This is really a beautiful case of the morphological independence of the larval state in insects. These characters, which are of a purely transitory nature, have never been in any sense adult structures, yet they have so thoroughly impressed themselves on the species, that they repeat their history in a very specific way in the development of the individual caterpillar.

On account of the small size and relatively unimportant function of the setæ, their use in classification is greatly enhanced. Thus the larger groups of Lepidoptera can be delimited more easily from a study of the larvæ than can those of most other insects, so far as our present knowledge extends.

Until very recently the pupæ of the Lepidoptera have not

received any general taxonomic treatment, although those of certain groups had previously been given attention by Packard and others, and those of many species had been described. As we should expect from the quiescent condition of the pupa it presents few characters other than those derived directly from the more or less fully developed external structure of the contained imago. Indeed, the cremaster, certain locomotory spines on the abdomen and tubercles on the thorax, are practically the only characters present which may be regarded as independent pupal modifications. Consequently, they are of much less interest than the larvæ, although Miss Mosher ('16) has been able to base, on the characters of the pupæ workable keys for identification of the families and of various groups of genera.

The Hymenoptera are perhaps the most remarkable group of insects in relation to their post-embryonic development as they are also in several other respects. In this group, as already stated, the larvæ of only the most generalized families, the saw-flies, retain the typical eruciform larva. They are in general appearance very much like Lepidopterous caterpillars, although differing at once in the minute structure of the legs and in the number of the abdominal ones. I am not aware that anyone has attempted a general classification of the saw-flies on the basis of larval structures although the larvæ of a large number of species have been described, and a very interesting account of the external anatomy has been given by MacGillivray ('13). Many are leaf-feeding in habits and show color patterns similar to those of the true caterpillars.

The larvæ of all the other groups of Hymenoptera are very greatly modified and hypermetamorphosis occurs in a number of cases.

Comparatively little is known of the larvæ of the several families of parasitic Hymenoptera, but those of some of the members of this group are very remarkable. In the later stages, nearly all are apodous, of very simple form, and without noticeable peculiarities. In the earlier stages, however, many strangely modified types are known which appear to be highly adapted to their mode of life. Some of these in which marked hypermetamorphosis occurs may be illustrated by Synopeas which has been

described and beautifully figured by Marchal ('06). Here the first larval stage which he has termed the Cyclops-larva is composed of an enormous cephalo-thorax, bearing a pair of absurdly enlarged jaws, and a slender abdominal portion. In the course of later development the abdomen enlarges, the jaws are cast off and the later stages assume the obese form characteristic of many larvæ of the higher Hymenoptera. Somewhat similar cyclopoid or highly modified larvæ are known to occur in a number of widely scattered genera and it will be doubtless found that this stage will greatly supplement any knowledge concerning the natural affinities of the very numerous and closely similar species. It is probable also that the structure of the larvæ will be found to reflect much more clearly the diversified behavior of these insects than does the structure of the imago.

As a rule the larger species of the parasitic Hymenoptera show less modification, but in a few of the small number of forms that have been studied, the early larvæ is provided with unusual structures of one kind or another. Most frequently the mandibles are noticeably enlarged.

Some of the members of this same group exhibit a very interesting phenomenon in the development of an early larva of typical campodeiform appearance which simulates very closely the first-stage larva of certain Meloid beetles and of the Strepsiptera. This hymenopterous planidium is, of course, not by any means identical with the triungulin in the other two orders, but presents many features in common with it. It will be noted also that it is the early larva and not the later one that is of the campodeiform type. The reason for the presence of a very active young larva is clear in all three cases, as the larva actually finds its own host, and is dependent upon its own resources at this early age. Here it is very evident that the planidium and triungulin have been interpolated in the larval development just as the whole larval stage has been added to the life-cycle of the metabolous insects. Their presence, especially in Hymenoptera is quite secondary.

Aside from those of the saw-flies, the larvæ of ants should be more susceptible to taxonomic treatment than those of other Hymenoptera. In general, these do not possess such remarkable modifications as occur in some of the parasitic families, but

the characters which they do have are apparently of such nature as to be suitable as a basis for classification.

The larvæ of the Coleoptera are probably, on the whole, more generalized than those of any other order of holometabolous insects. At any rate, the larvæ of the most primitive families, which are included in the suborder Adephaga, are campodeiform and in many cases similar to the adults. As in all larvæ, there are, of course, no wings and the trophi, antennæ, eyes and legs are much reduced and simplified. In the suborder Rhyncophora or snout-bettles, the larvæ are legless and much simplified in structure, and this condition prevails in a couple of other, evidently related families. For a long time the larvæ of beetles have attracted the attention of entomologists on account of their greatly diversified structure and interesting adaptations. At about the same time, two European zoölogists, Perris ('76) and Schiødte ('76–'83) published elaborate and beautifully illustrated systematic accounts of beetle larvæ, and made available a vast amount of material relating to these insects. Comparatively little was added to this for many years, but interest is again awakening in the matter.

The work of Schiødte and Perris shows very clearly that a complete classification of many families of beetles on the basis of the larvæ will be possible. As is well known to all entomologists, the larvæ of a good many groups are recognizable at a glance, from their general habitus alone. Of these one series representing the lady-birds or Coccinellidæ has recently been treated by Böving ('17) in a systematic way. These larvæ are active, predatory forms with well developed legs and with various tubercles, spines or processes developed on the thorax and abdomen. Böving has been able to develop a system of classification based upon many characters which appears to be very satisfactory, although limited as are all studies of this sort by the great difficulty in obtaining extensive series of larvæ that are accurately correlated with the imagines.

A very different type of Coleopterous larvæ occurs in the family Cerambycidæ, or longicorn beetles. In this group, the larvæ are legless, cylindrical creatures, undergoing their entire development in the woody tissue of various shrubs and trees.

Like all larvæ of similar habits they are of uniform white or buff color, except for the pigmentation of certain parts and appendages of the head. One could scarcely find any series of insect larvæ of more uniform appearance, yet we find that the structural and color characteristics of the adults of this enormous family are remarkably diverse and striking. In connection with their general work on beetle larvæ, Perris and Schiødte have examined some representative longicorn larvæ, but quite recently, two American entomologists, Webb ('12) and Craighead ('15) have attempted to classify these larvæ on structural characters. Although they have been restricted to a small number of details, mainly confined to the head, it appears that most of the genera may be distinguished more or less satisfactorily. The subfamilies (or families as they are called by Webb) appear also to be easily recognizable in the larvæ. If this proves still to be true as the larvæ of more genera and species are made known, it will be of particular interest, since such divisions are difficult on the basis of the imagines. We have seen that in most groups of insects the larvæ are generally less useful for the delimitation of larger groups than the adults.

Mention has already been made of hypermetamorphosis, and its occurrence in certain beetles noted. A closer examination of the larval stages of the Meloidæ shows, however, such a series of very evidently adaptive forms, that I cannot refrain from considering these somewhat in detail. The preparatory stages of various Meloids live upon the egg masses of certain locusts and within the larval cells of solitary bees, and several very distinct larval types succeed one another in the course of development. The parent beetle does not deposit her eggs directly in the materials which the larvæ is destined to devour, and the newly hatched Meloid larva is a tiny, active, long-lived creature that goes in search of its proper environment either by seeking out the locust eggs, or by attaching itself to the bee and thus being carried to its food. The triungulin is thus well-fitted to fulfill its mission and so far as its structure is concerned, presents nothing unexpected, for it is of the typical campodeiform type, widely distributed among insects. In the case of *Epicauta*, parasitic on locust eggs, shortly after reaching its food-supply,

the larva molts and assumes a second form with shorter legs and mandibles and soft skin; it is still distinctly of the campodeiform type, however, and similar to the larvæ of a number of other rather primitive families of beetles, and hence termed "caraboid" from the family Carabidæ. After another molt another larva appears, very similar to that of the family Scarabæidæ, and suitably known as the scarabæoid larva. The next stage is formed in a smooth cavity in the soil and is characterized by a more or less rigid, curved body; it is known as the coarctate larva and usually undergoes hibernation. In the spring, the next larva is a return to the Scarabæoid type which does not feed, but burrows about for a time and finally pupates after the manner of other beetles.

It is very evident that the several larval forms are beautifully adapted to the varied conditions which the larva has to meet during its development. They also follow a general course of degredation and loss of activity as their life cycle, reproducing in a general way the evident steps taken by evolution in the transition from the campodeiform to the apodous type. There is one anachronism, however, in relation to the scarabæoid larvæ. If, as appears to be true, this is really similar to the larva so named in the family Scarabæidæ, it can not bear any genetic relationship, since the Lamellicornia, to which the Scarabæidæ belong is a very highly specialized group which could not be derived from the otherwise greatly specialized Meloidæ that are the offshoot of another group of beetles. Likewise we cannot imagine a derivation in the opposite direction. We are forced, therefore, to the conclusion that this specific larvæ is only a response to similar stimuli in the environment in the two insects. Such a case serves well to illustrate that in larvæ as in adults the appearance of similar structures through convergence may easily lead to misconceptions. This example is more striking than the independent appearance of triungulin larvæ in widely separated groups, for as we have seen the triungulin is a very generalized larva of the campodeiform type.

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